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The distribution pattern of mire specialist butterflies in raised bogs of the northern lowlands of Central Europe

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Abstract. Raised bogs are extreme and azonal ecosystems with a characteristic hydrological balance, microclimatic conditions and a specific flora and fauna. Recently, these ecosystems have increasingly become the focus of scientific and general attention because of their important ecosystem roles in the face of global warming and providing biodiversity refuges. From a biogeographical and evolutionary context, the peat bogs of the European Lowlands serve as palaeorefugia, acting as cold, edaphic island habitats for arcto-alpine or boreo-montane insect species in temperate biomes. Analysing 105 peat bog sites in the northern lowlands of Central Europe, we compare the diversity and geographic distribution pattern of a subset of six butterfly species, which appear to be tyrphobiontic or tyrphophile mire specialists. We demonstrate a decrease in mean species number in the European Lowlands on a gradient from the east (Northern Belarus, about 4 species) to the west (Northern Germany, about 1 species), and suggest that the decreasing species number may be mainly caused by human impact in the past. The individual distribution pattern shows a nearly complete gap in occurrence of the sensitive bog specialist species *Colias palaeno* and *Boloria eunomia* in Northern Germany and an increasing presence of those species in peat bogs of eastern Europe. *Boloria aquilonaris* shows a different pattern, which, in contrast to *C. palaeno*, is continuously distributed in all sampled regions and seems to be the more tolerant of tyrphobiontic butterflies in the face of human impact on peat bogs. In the light of other recent findings our results also suggest that *Boloria aquilonaris* and *Plebejus optilete* may serve as target species reflecting success in ecological restoration of peat bog ecosystems.

Introduction

Raised bogs are extreme and azonal ecosystems with characteristic hydrological balance, microclimatic conditions and a specific flora and fauna (Mikkola and Spitzer 1983; Sushko 2012). The initiation of peat bogs in northern European young moraine regions began during the Early Holocene

and the development of raised bogs occurred during Mid- and Late Holocene climatic periods (Mauquoy and Yeloff 2007; Ruppel et al. 2013). Raised bogs and fens have important ecological functions in terms of hydrological balance, as well as storage of carbon dioxide and methane on local and global scales (Edom 2001). Whereas in Western Europe many countries have lost far more than 90% of intact peatland ecosystems due to human impacts, several countries in Eastern Europe have maintained between 15–50% of their natural peatland heritage (Bragg et al. 2003; Sushko 2012; Bonn et al. 2016). Recently, in light of numerous scientific studies regarding the role and function of peatlands in the global carbon and water cycles (e. g. Dorrepaal 2009; Kasimir et al. 2018 and references therein), there have been increased bog restoration efforts in many European countries; many of which have been supported by the European Union (Bonn et al. 2016). From a biogeographical point of view, raised bogs in Central Europe provide refugia for boreo-alpine species in a large scale temperate landscape and support the habitat preference of boreal or subarctic species mainly by climatic (cold) and edaphic (acidic and nutrient poor) conditions (Spitzer and Danks 2006; Sommer et al. 2015). During the climatic development from the Early to Late Holocene peat bogs remained "cold-lands" within the temperate biome and established patchy and isolated refugial habitats for cold adapted biota (Spitzer and Danks 2006; Sommer et al. 2015). The term "glacial relicts" is frequently used for boreo-montane species from peat bogs, especially by lepidopterists (Turlure et al. 2009, 2010). However, as there is no obligatory connection between these species and Pleniglacial or Late Glacial environments (Sommer et al. 2015), we suggest following Spitzer et al. (1999) and Spitzer and Danks (2006) in classifying peat bogs with cold adapted and tyrphobiontic insect species as "palaeorefugia" which indicate the colonization origin of this species and establishment of populations during past millennia of the Holocene. In this sense the butterfly *Boloria aquilonaris* and dragonfly *Aeshna subarctica* are typical cold-adapted species; isolated relict survivors in peat bog palaeorefugia (Sommer et al. 2015). As documented, in northern Germany, during the 19th and 20th centuries peatlands and raised bogs were increasingly degraded and drained by humans (Joosten and Couwenberg 2001; Heinecke et al. 2011; Thiele et al. 2015). For example, in northern Germany several tyrphobiontic butterfly species such as *B. aquilonaris* or *Plebejus optilete* experienced a strong decline or went extinct, as did *Colias palaeno* in historic times, due to peatland degeneration (Reinhard et al. 2014; Thiele et al. 2015, 2016; Meineke 2020; Caspari et al. 2020). These species also nearly disappeared from neighboring areas in Poland, i. e. from Western Pomerania (Buszko and Masłowski 2015). Accordingly, it has been suggested that cold adapted stenotopic butterfly species will increasingly suffer with future rising global temperatures (Settele et al. 2008; Thiele and Hoffmann 2017). Thus, in light of current climate change and efforts to restore peatlands (Noreika et al. 2016) it is important to have both current and historical information on environmentally sensitive target species in order to predict further developments of species distribution by modelling or adaptation of conservation strategies locally and globally. Here we analyse the distribution pattern of mire specialist butterflies along a west-east gradient in the Central European lowland regions.

Material and methods

We selected a subset of six species that are mire specialists after Noreika et al. (2016). These species (*Colias palaeno*, *Oeneis jutta*, *Boloria aquilonaris*, *Boloria eunomia*, *Coenonympha tullia* and *Plebejus optilete*) show a regularly presence in peat bogs in the young moraine areas of northern

Germany, northern Poland, Lithuania and northern Belarus and have mainly a boreo-montane distribution pattern. In Central Europe these species show a strong association with peat bogs. Several of these species, for example *B. eunomia* or *C. palaeno* appear to have relict distributions, restricted to palaeorefugia in Central and Northern Europe (Nève et al. 2009; Krzysztofiak et al. 2010; Turlure 2010; Sommer et al. 2015). The Bog Fritillary *B. eunomia* is not restricted to raised bogs but also inhabits pine bogs, fens and marshes and the ecotone regions between bogs and fens (Nève et al. 2009; Noreika et al. 2016; Sielezniew et al. 2019). We analysed a dataset of records of the six selected mire specialist butterflies from 105 raised bogs in the European Lowlands (Fig. 1 and Table 1). The studied region for the countries mentioned above is mainly a function of the research activities on Lepidoptera by the authors of this paper. In these regions, over the last 20 years, peat bog sites with a potentially promising insect fauna (including Lepidoptera, Coleoptera and dragonflies) were selected and regularly recorded along transects lines. Every site was visited during three to five different years regularly during the flight period in June to August. The transect lines (1–3 km in length) represent the most important habitats for each site, and accordingly differ in size. Only the species inventory of insect populations is compared between the sites and no quantitative information is given. We compiled presence/absence records for the six selected species (from peat bog site) (Table 2, Suppl. material 1: Table S1 and Fig. 1). Percentage frequencies of occurrence were calculated to evaluate the consistency of species in the sites in each focused region. We used absence/presence data for our data assessment to ensure comparability (because of differences in the number of field surveys and extent of sampled transects). However, as our data are based on numerous samplings from each site in different seasons, over the last 20 years, taken by very experienced experts in the field. Thus, the broad picture of presence/absence should be reliable. We determined a gradient in species richness from west (NW Germany, NE Germany) to east (NE Poland, Lithuania, N Belarus) in the northern lowlands of Central Europe (Table 1 and Fig. 1). Additionally, we assessed the local presence of species to determine the differences in species patterns and the depletion of fauna from a geographical point of view. From our large sampling area and available regional context information, we reviewed the selected species in the light of a possible geographical gradient in the degree of association with peat bogs. The observed regional degree of association with peat bogs is assigned to the different species in four different categories that are displayed in Table 3: 1. tyrphobiontic *sensu stricto* (exclusively restricted to peat bogs), 2. tyrphobiontic *sensu lato* (tyrphobiontic to tyrphophilous), 3. tyrphophilous (preferentially occurs in bogs but also other habitats) and 4. frequently present in but not obligatory associated with peat bogs. For calculating mean species richness per site, frequency of occurrence, standard errors, standard deviation and data plots we used the software program "Past", version 3.25, 05/2019 (Hammer et al. 2001).

Table 1. Overview of spatiotemporal sample coverage of data from butterflies from raised bog sites in the European Lowlands. For detailed information on individual sites see Suppl. material 1: Table S1. For geographical positions of sites see Fig. 1. For more specific information on the individual localities see Suppl. material 1: Table S1.

Country	Region (federal state)	Evaluated peat bog sites	Time period
Germany	Northwest (Schleswig-Holstein)	16	2000–2017
Germany	Northeast (Mecklenburg-Western Pomerania)	28	1998–2017
Poland	mainly northeast	18	1999–2018
Belarus	Northern	12	2000–2015
Lithuania	Complete	31	1999–2014

Results

The inventory of six selected tyrphobiont species from 105 raised bogs in our investigation area shows remarkable differences in individual species composition and species richness along a gradient from western to eastern Europe (Fig. 1, Table 1). In Western Europe the mean number of species per site was low (NW Germany 1.12 and NE Germany 1.14) in contrast to Eastern Europe (northern Poland 2.27, Lithuania 3.03 and Belarus 4.00) (Table 2, Fig. 2b). Two to three species are regularly recorded from NW and NE Germany, whereas up to six are recorded from the eastern European countries (Table 2). Fig. 2a displays the number of recorded species from each site and shows highest values for NW and NE Germany of up to three species per site, whereas there are 4–6 species in NE Poland, Lithuania and Belarus (Figs 1, 2a). The individual species patterns are given in Table 2 and Fig. 3a–f. The pattern of the tyrphobiontic species *C. palaeno* and *B. eunomia*, extinct in Northern Germany, shows a very similar trend with increasing occurrence from west to east (Table 2. Fig. 3a, c). *Oeneis jutta* is absent from Germany but shows increasing frequency along a west to east gradient (s. Table 2, Fig. 3f). In contrast, the other strongly tyrphobiontic species, *B. aquilonaris*, is present in all regions (Fig. 3b), although in NE Germany the frequency is below 50% (Table 2). In Northern Germany only two of the bog-associated species show an uninterrupted, continuous occurrence: the tyrphobiont *B. aquilonaris* and the tyrphophilous *C. tullia* (Table 2).

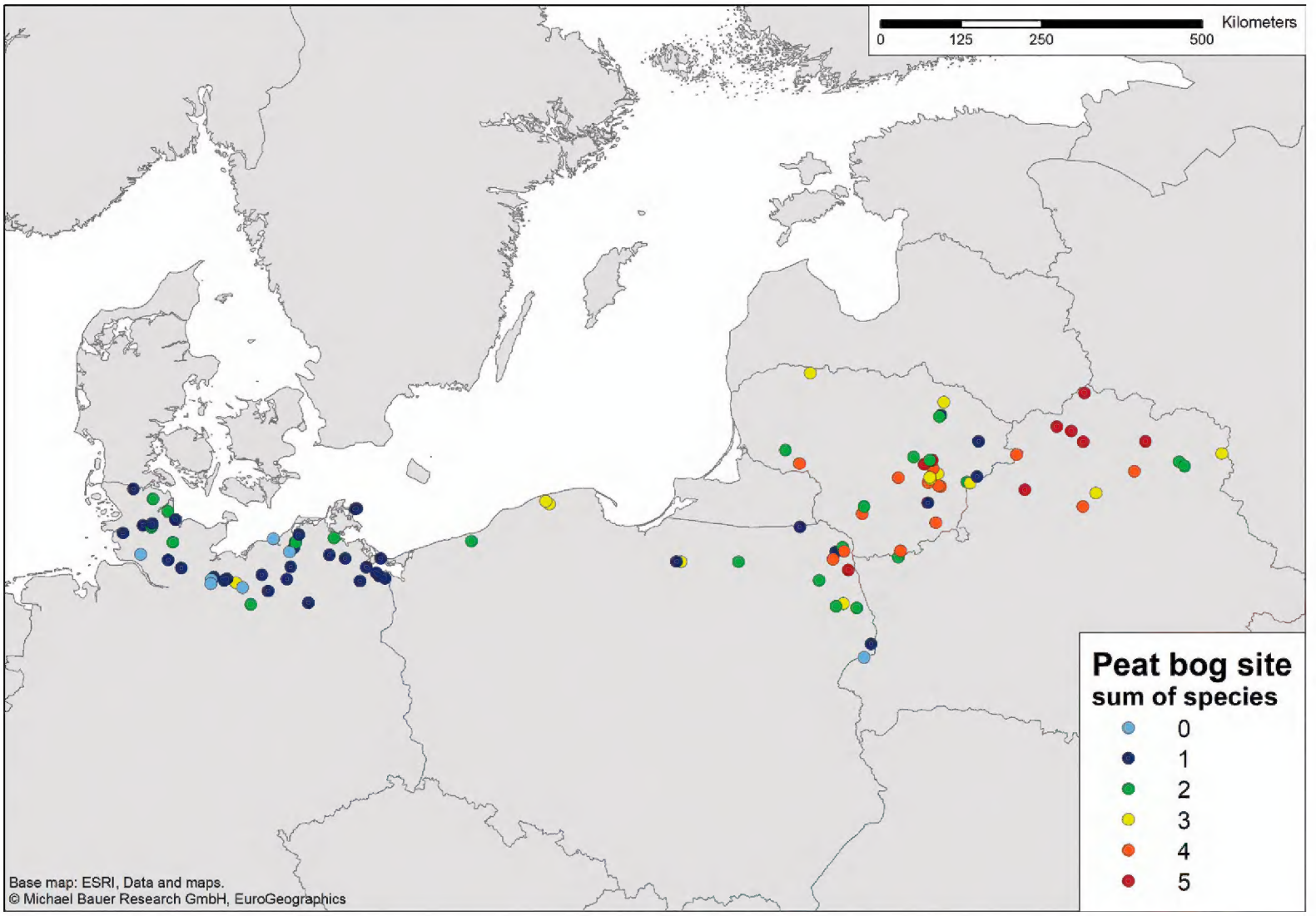

Figure 1. Geographic covering of sample sites (raised bogs) in the northern lowlands of Central Europe and number of selected tyrphobiontic/tyrphophile butterfly species. For selected species see Table 2.

Table 2. Number of sites with presence of a certain species ("sites") and percentage frequency of occurrence of a species (% occ.) in raised bogs of a particular region of the European Lowlands (Fig. 1). The number of investigated sites is displayed beneath the region/country. (*the species has no autochthonous distribution in this region).

Species	NW Germany		NE Germany		NE Poland		Lithuania		N Belarus	
	N = 16 sites		N = 28 sites		N = 18 sites		N = 31 sites		N = 12 sites	
	sites	% occ	sites	% occ	sites	% occ	sites	% occ	sites	% occ
Colias palaeno	0*	0*	0	0	9	50.0	29	93.5	11	91.7
Boloria eunomia	0*	0*	1	3.6	7	38.9	20	64.5	12	100
Boloria aquilonaris	8	50.0	9	32.1	10	55.6	19	61.3	9	75.0
Plebejus optilete	0	0	8	28.6	10	55.6	20	64.5	8	66.7
Coenonympha tullia	10	62.5	14	50.0	3	16.7	0	0	0	0
Oeneis jutta	0*	0*	0*	0*	2	11.1	6	19.4	8	66.7
mean species/site	1.125		1.142		2.277		3.032		4.000	
sum of species	2		4		6		5		5	
std. errors (SE)	0.179		0.122		0.300		0.214		0.348	
std. deviation (SD)	0.718		0.650		1.274		1.196		1.206	

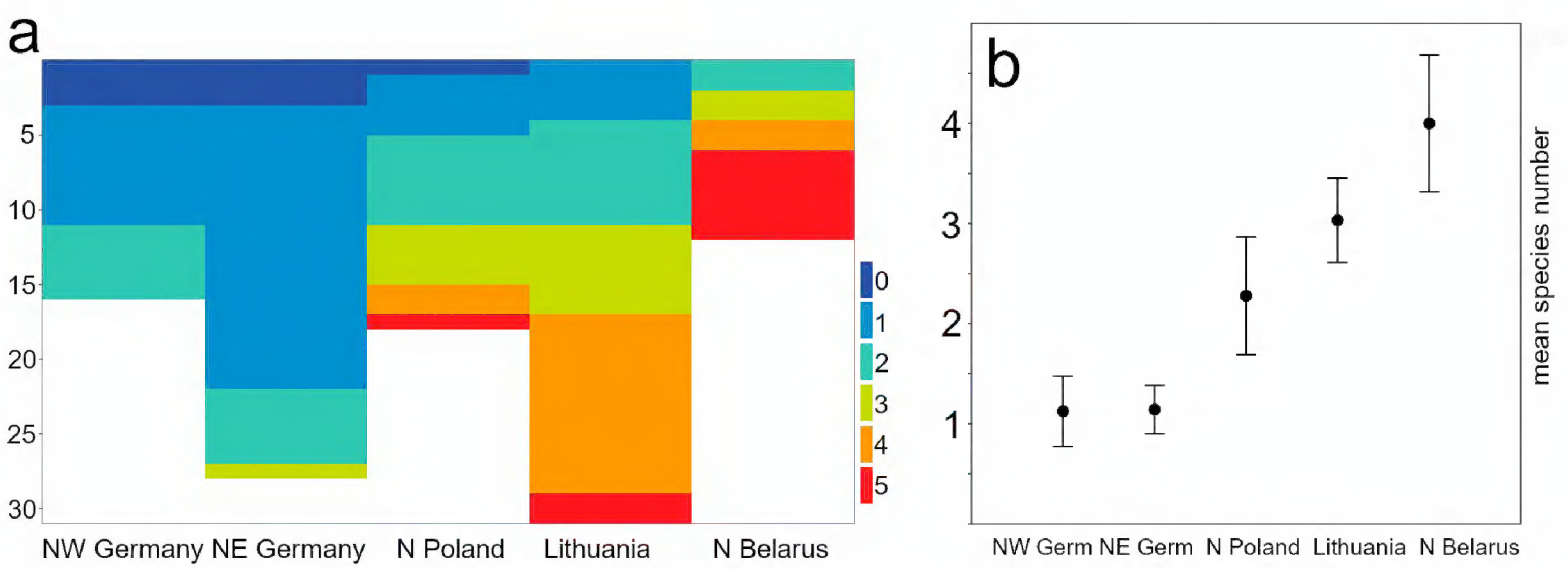

Figure 2. Number of sampled peat bog sites and recorded species per site. (**a**) Number of peat bogs surveyed per study area (y-axsis). The number of species from single sites are keyed with different colors in the bar plots (see legend at the right margin). (**b**) Mean species number (whisker represent the standard error) from raised bogs in different regions.

Discussion

Individual species distribution patterns and regional habitat association

The individual spatial pattern of species, habitat preferences and zoogeographical traits (refugia etc.) of tyrphobiontic/tyrphophile butterflies are the key for understanding changes in distribution dynamics over time. In this context, data for the Moorland Clouded Yellow *C. palaeno* is of great interest for zoogeography and conservation ecology. *C. palaeno*, with its strong preference for open vegetation, went extinct during the first half of the 20th century in north eastern Germany due to the severe human impact on peat bogs (Thiele et al. 2015). Recently, its distribution in Germany is restricted with numerous populations to the far south of Baden-Württemberg and Bavaria as well as Saxony (Kolligs 2009; Anwander et al. 2013; Thiele et al. 2015; Dolek and Georgi 2017; Hafner 2020). In eastern Europe the extent of past degradation of wetlands was much lower and so *Colias palaeno* experienced less decline in Poland. Further east in Lithuania and Belarus the

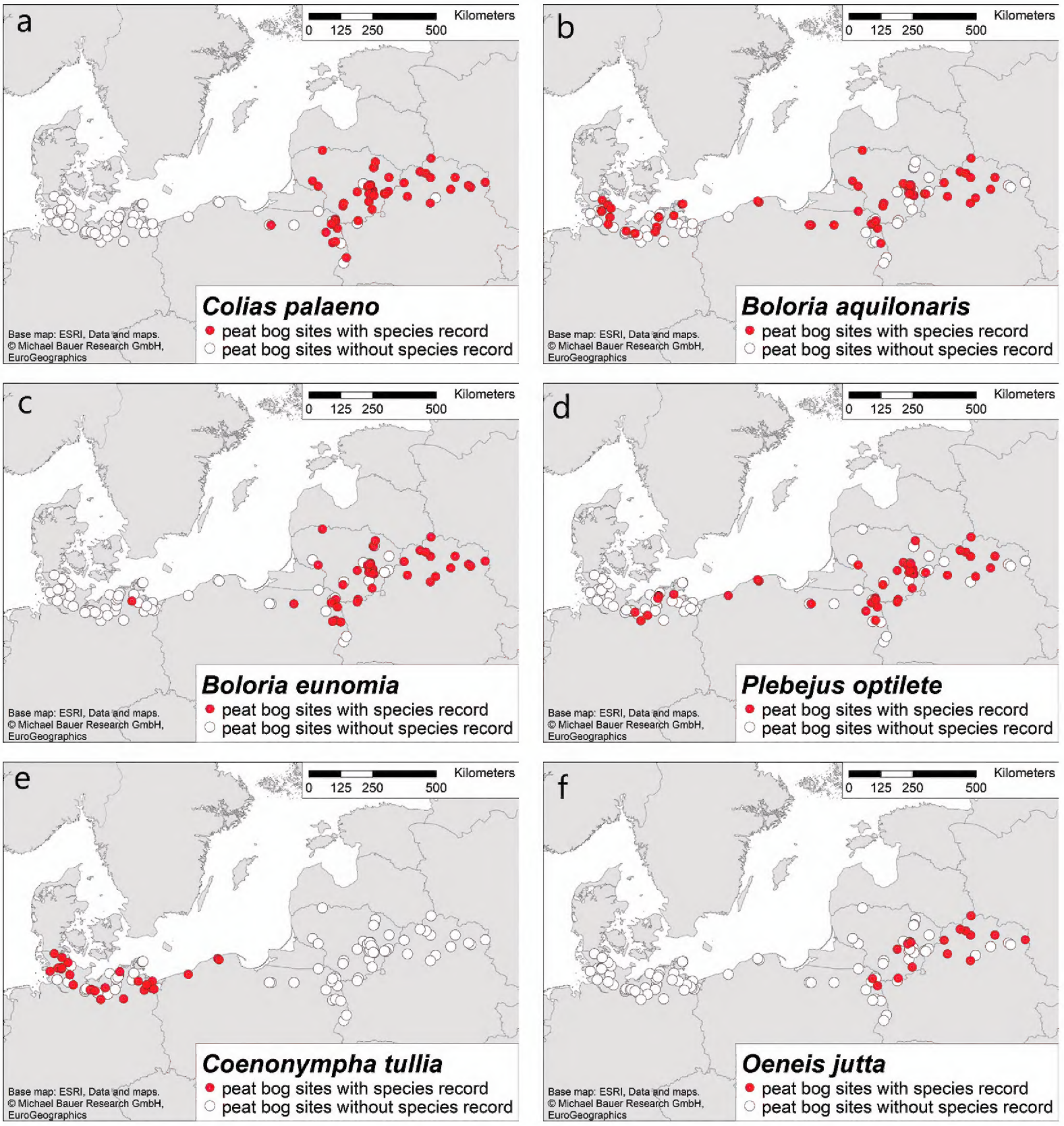

Figure 3. Absence (white dots) and presence (red dots) of *Colias palaeno* (**a**), *Boloria aquilonaris* (**b**), *B. eunomia* (**c**), *Plebejus optilete* (**d**), *Coenonympha tullia* (**e**) and *Oeneis jutta* (**f**) in our 105 sampling sites in the northern lowlands of Central Europe.

species is common and frequent in peat bogs (Dapkus and Švitra 2001, Fig. 3a). Recent studies on *B. eunomia* show that in the eastern part of the area there are two distinct ecotypes which use different larval food plants; i. e. *Bistorta major* on wet meadows and *Vaccinium oxycoccus* (and possibly also other ericaceous plants) on raised bogs. Recent findings suggest that the meadow form is ancestral (Klimczuk and Sielezniew 2020). Interestingly, our data show similar distribution pattern of *C. palaeno* and *B. eunomia* in raised bogs in northern Europe (Fig. 3a, c). The recent Palaearctic distribution pattern of *B. eunomia* in Europe is very similar to that of *C. palaeno* (Kudrna

et al. 2015) and this is confirmed also by our data of *C. palaeno* and *B. eunomia* in raised bogs in northern Europe (Fig. 3a, c). However, the relictual distribution in peat bogs in northern Europe which are refugia in a highly fragmented European range may be a consequence of general habitat loss of wet meadows, fens, bogs together with overly mild winter temperatures (Schtickzelle et al. 2007; Twelbeck and Reinhardt 2020). The Cranberry Fritillary *B. aquilonaris*, thought to be a mire specialist in Scandinavia (Noreika et al. 2016) and strongly associated with peat bogs (as palaeorefugia) in Central Europe (Turlure et al. 2010; Thiele and Luttmann 2015), together with the Cranberry Blue *A. optilete* are the only mire specialist species (Noreika et al. 2016) also present in the raised bogs of NW and NE Germany (Fig. 3b, d). *B. aquilonaris* seems to be more tolerant and ecologically flexible in the face of bog degeneration than is *C. palaeno*, as the former was recorded from peat bogs with significant human impact (Thiele et al. 2015; Bönsel and Sonneck 2016). An explanation for this may be that *B. aquilonaris* is more dependent on heterogeneity of habitats than the size of peat bog, as suggested by Thiele (2006) and Bönsel and Sonneck (2016). *B. aquilonaris* also occurs in smaller bogs with partial forest covering and this species is generally more tolerant towards human impact than the *P. optilete*. Nevertheless, the sensitivity of *B. aquilonaris* to human impact on peat bogs resulted in 50% local extinctions during historical times of the peat bog sites from northwestern Germany (Suppl. material 1: Table S1). In Poland *B. aquilonaris* inhabits both peat bogs and transitional mires. The most important factor is the abundance of *V. oxycoccus* in open areas of the larval food plant. Unlike *B. aquilonaris*, *P. optilete* is extinct in NW Germany and several cases are documented where it was formerly present in selected peat bog sites in NW Germany in past decades of the 20th century (Suppl. material 1: Table S1). The Large Heath *Coenonympha tullia* is known as a mire specialist in Europe (Weking et al. 2013; Thiele and Luttmann 2015; Noreika et al. 2016). However, although the geographic range covers our whole sampling area in the European Lowlands (Kudrna et al. 2015, Fig. 1), it is striking that the species is absent in raised bogs east of the river Vistula in Poland and the other focused regions of eastern Europe (Fig. 3e). For a long time, *C. tullia* was considered as a bog species however (Weking et al. 2013 and references therein). Weking et al. (2013) discovered that *C. tullia* has a twentyfold density in managed (but undrained) fens with a dominance of broad-leaved bog-cotton *Eriophorum latifolium*. Therefore, *C. tullia* is not a tyrphobiontic species in all parts of the northern Lowlands of Central Europe (see Table 3), also suggested by Nunner and Bolz (2013) for Bavaria. An explanation for the lack of *C. tullia* in Eastern European raised bogs could be the abundance of pristine fens managed by traditional mowing. In western Europe, a substantial decrease of 20–50% for this species occurred during times of intensive mire draining during 1970–1995 (Van Swaay and Warren 1999). Therefore, peat bogs may increasingly serve as suboptimal refugial habitats. In some areas of N Poland *C. tullia* is restricted to fens although raised bogs are available nearby. This phenomenon could be related to the larval food plant choice, *Carex* spp., which are rather rare in raised bogs but abundant in fenland communities. The Jutta Arctic *O. jutta* is a boreal species. Our records show the most southwestern distribution in Europe (Fig. 3f), which includes eastern parts of Poland (Krzysztofiak et al. 2009, 2010). It is not known whether *O. jutta* was present in historical times in western Europe or how far its range declined in northern Poland (cf. Krzysztofiak et al. 2009, 2010). Accordingly, in the light of recent literature on habitat preferences of species in the European lowlands, we present an overview of the degree of regional association with peat bogs of the selected species (Table 3). The literature data as well as the experiences from our sampling regions show that degree of peat bog association may differ according to geographical region and

Table 3. Observations about differences in habitat preferences and peat bog association of diurnal butterfly species along a geographic gradient from western to eastern parts of the European Lowlands. Categories of habitat association following Thiele and Luttmann (2015) and Weking et al. (2013). **Legend:** ++++ tyrphobiontic *sensu stricto* (exclusively restricted to peat bogs), +++ tyrphobiontic *sensu lato* (tyrphobiontic to tyrphophilous), ++ tyrphophilous (preferentially occurs in bogs but also other habitats), + frequently present in but not obligatory associated with peat bogs. NAD = no autochthonous distribution. (* two different ecotypes of *B. eunomia* show different habitat association (Sielezniew et al. 2019). DD = data deficient.

Species	Palaearctic distribution	NW Germany	NE Germany	N Poland	Lithuan	N Belarus
Colias palaeno	boreo-montane	NAD	++++	++++	++++	++++
Boloria eunomia	boreo-montane	NAD	DD	++/++++*	+++	++++
Boloria aquilonaris	boreo-montane	++++	++++	+++	+++	++++
Plebejus optilete	boreo-montane	++++	++++	++++	++++	++++
Coenonympha tullia	N palaearctic	++++	+			++
Oeneis jutta	boreal	NAD	NAD	++++	++++	++++

environmental context. For example, *C. palaeno* shows a marked restriction to peat bogs and is strongly tyrphobiontic in most Central European areas (Thiele and Luttmann 2015; Dolek and Georgi 2017), while above the treeline in the Alps dwarf shrub communities are utilized as habitats (Dolek and Georgi 2017). In Finland, *C. palaeno*, *C. tullia* and *P. optilete* fall into class 2 of mire specialists, which means that 50–95% of populations occur in mires. However, *O. jutta*, *B. eunomia* and *B. aquilonaris* are grouped in class 1, as over 95% are in mires (Pöyry 2001; Kullberg et al. 2002).

Species richness and target species for peat bog restoration in northern Germany

With the exception of *O. jutta*, whose Palaearctic range covers only the eastern part of our sampling range (Fig. 3f) (Kudrna et al. 2015), all species of the selected subset of mire specialists are distributed within our sampling area (Table 2, for further information on distribution status and habitat preferences see Suppl. material 1: Table S2). The number of species in single peat bog sites (Fig. 2a), the mean species number at sites in a region (Fig. 2b) and the percentage frequency (Table 2) clearly indicate a decreasing number of mire specialist species from eastern to western Europe (Fig. 1). We suggest that the decreasing species richness from eastern to western parts of the northern lowlands of central Europe may reflect the (degree of) degradation of natural conditions of peat bog ecosystems in general. The countries of western Europe have lost far more than 90% of intact peatland ecosystems due to human impact. In contrast, several eastern European countries have retained between 15–50% of their natural peatland heritage (Bragg et al. 2003; Sushko 2012; Bonn et al. 2016). The remaining area of former natural peatland ecosystems in Germany is about 1%, in Poland 15%, in Lithuania 40% and in Belarus about 45% (Joosten and Couwenberg 2001). Interestingly, the pattern reported here of decreasing species richness (Fig. 2b) and decreasing numbers of mire specialist butterflies in single peat bog sites, respectively, from eastern to western parts of the northern lowlands (Fig. 1, 2a) roughly coincides with the decreasing availability of natural peatland ecosystems along this geographical gradient.

We suggest that *B. aquilonaris* and *P. optilete*, two mire specialist species that have survived even in several degraded bogs of northern Germany and other Baltic regions (Bönsel and Sonneck 2016; Thiele and Hoffmann 2017), may serve as target species for peat bog restoration approaches

in western countries of the northern lowlands of Central Europe. As representatives for tyrphobiontic insects, specialised on various successional stages in peat bogs, both species together are suited as bioindicators reflecting positive changes (reopening, changes in heterogeneity of vegetation, rising water level and peat regeneration etc.) of biodiversity in peatbogs after restoration. Both species are tyrphobiontic *sensu stricto* and highly threatened by draining, degradation and afforestation of peat bogs. A further argument is that *B. aquilonaris* and *P. optilete* show higher ecological flexibility than other mire specialists (e.g. *C. palaeno* or *B. eunomia*) and in recent decades have not suffered a strong decline in Germany (Anwander 2013a, b). After hydrological restoration and deforestation of peat bogs *B. aquilonaris* is able to colonize quickly open patches of former peat cutting holes (Anwander 2013a; Thiele and Hoffmann 2017). In contrast to *B. aquilonaris*, *P. optilete* is able to use a wider spectrum of plant species as larval habitat and seems to be more tolerant to restricted availability of flowering plants within its home range (Anwander 2013a, b). Of all mire specialist butterflies across the entirety of the northern lowlands of Central Europe, *B. aquilonaris* and *P. optilete* are the most widely distributed. However, in the focal area in northern Germany, there are only five sites known where both species occur together (Suppl. material 1: Table S1) and in NW Germany, *P. optilete* is completely absent. Accordingly, both are represented in nearly all our sampling regions and recorded regularly (albeit at times fragmentarily) in various regions of northern Germany. Thus, based on the ecological and biogeographical context, we suggest that with ecological restoration of peat bogs in northern Germany and adjacent western European countries of the European lowlands as havens for specialized insect species, the presence of both candidates may effectively represent positive developments in times of global warming.

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Supplementary material 1

Tables S1, S2

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Data type: Table.

Explanation note: Table S1. Localities and geographic coordinates of the investigated peat bog sites, species composition of detected peat bog associated diurnal lepidopterans, year of investigation or publication, involved scientists and References. Table S2. Climatic- and habitat preferences as well as information on faunal status of the focal species. The information on habitat preferences are restricted to populations of the northern lowlands of Central Europe.

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